

COMPETITIVE RESPONSE OF NATIVE *SOLIDAGO ALTISSIMA* (LATE
GOLDENROD) AND INVASIVE *TANACETUM VULARE* (COMMON TANSY)
DIFFER ACCORDING TO PLOIDY AND GENOTYPE

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ABSTRACT

It is becoming increasingly important for us to understand the ability of native plant populations to tolerate competition by invasive species. The ability to contend with the presence of an invader may depend on the genetic structure of both the native and invading population. This study examines the roles of polyploidy, genetic variation in growth traits, and variation in plasticity in response to the presence of competition in determining competitive outcomes. I examined the genetic architecture from both sides of the competitive interaction between native diploid and tetraploid genotypes of *Solidago altissima* (late goldenrod) and genotypes of the invasive species *Tanacetum vulgare* (common tansy). In this study, both ploidy level and the specific genotype within ploidy level of *S. altissima* influenced the outcome of the competitive interaction, with tetraploids being better able to suppress the growth of the invasive species to a greater extent than diploids. In addition, some tetraploid genotypes expressed adaptive plasticity such that they were able to tolerate the presence of *T. vulgare* and maintain growth. Similarly, genotypes of *T. vulgare* differed in their competitive ability when paired with diploid or tetraploid *S. altissima*. Overall, this work suggests that both species possess genetic variation such that competitive ability may evolve in response to the presence of the other species. This underscores the importance of examining both sides of a competitive interaction to understand the complex evolutionary dynamics that occur between native and invasive plant species.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS.....	<i>i</i>
ABSTRACT.....	<i>ii</i>
TABLE OF CONTENTS.....	<i>iii</i>
LIST OF TABLES.....	<i>iv</i>
LIST OF FIGURES.....	<i>v</i>
INTRODUCTION.....	1
MATERIALS AND METHODS.....	5
RESULTS.....	11
DISCUSSION.....	17
LITERATURE CITED.....	22
TABLES AND FIGURES.....	27

LIST OF TABLES

TABLE

1	Target <i>Solidago altissima</i> end-of-season analysis.....	27
2	Target <i>Solidago altissima</i> repeated measures analysis.....	28
3	Intraspecific Competitor <i>Solidago altissima</i> end-of-season analysis.....	29
4	Intraspecific Competitor <i>Solidago altissima</i> repeated measures analysis.....	30
5	Interspecific Competitor <i>Tanacetum vulgare</i> end-of-season analysis.....	31
6	Interspecific Competitor <i>Tanacetum vulgare</i> repeated measures analysis.....	32

LIST OF FIGURES

FIGURES

1	Representation of one pot in each of three competition treatments.....	33
2	Representation of 6 randomized blocks.....	34
3	Effect of three competitive treatments on target <i>S. altissima</i>	35
4	Effect of competitive treatments on genotypes of target <i>S. altissima</i>	36
5	Effect on competitor traits by ploidal level of target <i>S. altissima</i>	37
6	Effect on <i>T. vulgare</i> genotypes depending on ploidal level of target <i>S. altissima</i>	38

INTRODUCTION

The outcome of ecological and evolutionary dynamics between invasive and native species depends critically upon the genetic structure of populations on both sides of the competitive interaction (Sakai et al. 2001, Lee 2002). This is because genetic variation within populations of either species underlies the potential for evolution of traits that enhance competitive ability. In other words, genetic variation may permit adaptive evolution on the part of either the invader or the native species (or both) in response to competition from the other. Furthermore, genetic variation in *response* to the presence of the competitor (G x E) may allow both native and invasive plants to evolve adaptive plasticity that allows fitness to be maintained even in the presence of a competitor (Schlichting 1986). Thus, it is important to examine the genetic structure from both sides of competitive interaction because findings of genetic variation for relevant traits and plasticity in those traits in both species indicate that co-evolutionary dynamics could ensue.

Genotypic diversity within a population is important for both sides of competitive interaction. Variation of different genotypes may facilitate a native population's ability to persist in a habitat and ability to tolerate invasion. For a native plant population, genetic diversity allows populations to be viable and evolve since genetic variability allows a population to efficiently use microhabitats, survive stochastic threats such as invasion, and maintain fitness for obligate out-crossing species (Falk and Holsinger 1991, Reed and Frankham 2003). As an example, Crustsinger et al. (2008) found that intraspecific diversity in *Solidago altissima* can deter plant invasions. Also, there may be more

chances for a strong competitor to combat invasion within a population with high genetic diversity. For invasive species, genetic variation is important because variation in founders may influence colonization success and successful range expansion in the introduced area (Falk and Holsinger 1991, Sakai et al. 2001). There may be more chances for a strong competitor to invade a new range within a founding population that is genetically diverse.

Just as important as genetic variation is the variation in genotypic plasticity to different environmental conditions. Studies have that shown that small-scale environmental heterogeneity leads to maintenance of genetic difference (Nevo et al. 1986, Linhart and Grant 1996, Lenssen et al. 2004). This indicates that there are some genotypes that more efficiently use microhabitats than other genotypes. In terms of a native population surviving stochastic events, greater variation in plasticity may counteract negative effects of temporal changes in the environment while still maintaining fitness (Falk and Holsinger 1991). Plasticity may also be an important factor in the success of an invasive species. Low levels of genetic diversity are seen in many invasive plant populations, and the success of these populations may be attributed to the pre-adapted capacity for high phenotypic plasticity in different environments in their source populations (Ward et al. 2008).

An added dimension of genetic structure that is relevant to many native species is polyploidy, or genome duplication. Polyploidy is common in plants, with frequency estimates in angiosperms that range from 30% to 80%, most estimates being around 50% (Stebbins 1950, Masterson 1994, Soltis and Soltis 2000, Soltis et al. 2009). Polyploidy

may confer a competitive advantage due to increased heterozygosity that could mask deleterious recessive mutations, novel genome rearrangements, and diversification of function in duplicated genes (Soltis and Soltis 2000, Comai 2005). In support of polyploidy advantage, elevated photosynthetic rates and capacity per cell were exhibited in hexaploid *Solidago gigantea* and *Atriplex confertifolia* compared to diploid counterparts (Warner and Edwards 1993, Hull-Sanders et al. 2009).

The objective of this study was to investigate the ecological effect of invasive species at the individual plant level. I examined the genetics of both sides of a competitive interaction between the widespread invasive perennial *Tanacetum vulgare* (common tansy) and the native polyploid perennial *Solidago altissima* (late goldenrod). The competitive ability of *T. vulgare* has not been well-studied, but it appears to be a good competitor based upon its extensive spread since its introduction to North America. In addition, *T. vulgare* is known to have insect-repelling compounds that may have an allelopathic effect on neighboring plants (Schearer 1984, Hethelyi et al. 1991, Gabel et al. 1992, Chiasson et al. 2001, Judzentiene and Mockute 2005).

The competitive ability of *S. altissima* has been studied numerous times, but in no case was ploidy level a focus in the studies (Goldberg 1987, Goldberg 1988, Walck et al. 1999). *Solidago* growth seems to be negatively affected by competition. A field study of *S. canadensis* in Michigan found inhibition by the presence of neighbors. Plants grown with neighbors had biomasses of 38% to 83% of plants grown without neighbors (Goldberg 1987). Similarly, a second study conducted in Michigan reported that *S. canadensis* had a higher probability of survival and flowering when competition was

reduced (Goldberg 1988). Allelopathy in *Solidago* has also been documented (Butcko and Jensen 2002). Even though *Solidago* is invasive in Europe (native range of *T. vulgare*), it does not appear to have greater competitive ability due to allelopathy (van Kleunen and Schmid 2003). In a common garden experiment, van Kleunen and Schmid (2003) found that European plants produced smaller inflorescences and fewer vegetative growths than the native American plants. This suggests that competition with a weedy exotic such as *T. vulgare* may alter the natural habitat of *S. altissima* and reduce plant size, alter the timing of flowering and reduce survival rates.

My main objective was to determine whether native *S. altissima* polyploids had an inherent advantage over their diploid counterparts in competition with invasive *T. vulgare*. I also tested whether there were differences among genotypes within ploidal level in their competitive ability against *T. vulgare*. From the invasive species perspective, I tested how genotypes of *T. vulgare* were affected by the presence of diploid or tetraploid *S. altissima*. In order to determine if differences were due to competition in general or due to competition specifically with *T. vulgare*, I tested intraspecific competition by diploid *S. altissima*. This allowed me to determine whether diploid and tetraploid *S. altissima* differ in their competitive ability against an interspecific invasive competitor *T. vulgare* versus competing against conspecifics.

MATERIALS AND METHODS

Study species

This experiment examined the competitive dynamics between a pair of co-occurring species of perennial rhizomatous herbs, the North American native polyploid *Solidago altissima* L. (late goldenrod) and the Eurasian invasive *Tanacetum vulgare* L. (common tansy). Both species have wide geographic ranges that overlap in all but seven U.S. continental states (Werner et al. 1980, Semple and Cook 2011, Watson 2011). *T. vulgare* is native to Europe and Asia and was introduced to North America as early as 1638 for medicinal and funerary purposes due to its antibacterial and antifungal compounds (Keskitalo et al. 1998, White 2002, LeCain and Sheley 2006). By the turn of the 20th century, *T. vulgare* was widespread in the upper Midwest (Voss 1996) and reached California in 1952 (LeCain and Sheley 2006). These early successional species are often found in the same plant communities; each colonizes disturbed habitats such as abandoned farmland, roadsides, and old fields (Rebele 2000, Weber 2000, White 2002).

S. altissima is a polyploid species with diploid ($x = 9$, $2n=18$), tetraploid ($2n =36$), and hexaploid cytotypes ($2n=54$) that occurs throughout the Midwest of the United States (Halverson et al. 2008). All-diploid populations are just as common as mixed-cytotype populations; however cytotypes occur at variable frequency both within and among populations in the Midwest (Halverson et al. 2008). In contrast, *T. vulgare* is primarily diploid ($x=9$, $2n=18$), although some higher chromosome counts have been reported in the native European range (Tropicos 2014).

Competitive dynamics between these species are likely to be intense both above and below-ground. *S. altissima* and *T. vulgare* spread vegetatively via rhizomes which are usually produced at the base of the current year's shoot in late autumn and lie dormant in winter (Cain 1990, White 1997). Rhizome pattern and growth in *S. altissima* can be highly variable: they could be sparse or densely packed (Maddox et al. 1989, Cain 1990). There is likely a tradeoff between rhizome number and length; rhizomes tend to be short and numerous when colonizing a new space (Hartnett & Bazzaz 1983). Rhizomes of *T. vulgare* are tightly coiled and do not extend over long distances because of the short lengths between connecting rhizomes (White 1997). Rhizomes of both species break dormancy in mid-April in Ontario (Werner et al 1980, White 1997).

In the study area, *S. altissima* and *T. vulgare* achieve similar heights ranging from 1 to 1.5 meters (MN DNR 2003), which suggests that these species compete for light. *S. altissima* is less shade tolerant, producing 7% less biomass under moderate shading (Cornelius 1990), whereas *T. vulgare* can occur in shady riparian zones (White 1997). Both species bloom from mid-July to the end of the growing season. Both species are outcrossers (Werner et al. 1980, Keskitalo et al. 1998) and rely upon generalist pollinators; for *T. vulgare*, flies, hover flies, butterflies, moths, and honey bees (LeCain and Sheley 2006) and for *S. altissima*, honeybees, bumblebees, soldier beetles and syrphid flies (Werner et al. 1980).

Experimental Design

I examined plant response to intra- and inter-specific competition from both sides of the competitive interaction between *T. vulgare* and the two locally common cytotypes

of *S. altissima*, diploids and tetraploids. The central questions were: 1) Do diploid and tetraploid *S. altissima* differ in their competitive ability against the Eurasian invader, *T. vulgare*? 2) Do genotypes within the two ploidy levels of *S. altissima* differ in their response to competition such that adaptive plasticity in response to competition could evolve? 3) Do *T. vulgare* genotypes differ in their competitive ability against diploid and tetraploid *S. altissima*? 4) Do genotypes of *T. vulgare* differ such that adaptive plasticity in response to competition could evolve?

The reciprocal effects of competition between *S. altissima* and *T. vulgare* were examined for two years using competitive arrays in which a single target plant (diploid or tetraploid *S. altissima*) was grown with: 1) no competition, 2) interspecific competition with three clones of *T. vulgare*, and 3) intraspecific competition with three clones of diploid *S. altissima* (year 2 only). In each year, the target *S. altissima* planting included five diploid and five tetraploid genotypes that were cloned and planted into competitive and non-competitive environments. Genotypes of the competitors were also cloned such that each competitor genotype was exposed to both diploid and tetraploid target *S. altissima*. Every competition-treatment pot had three competitor clones planted in a tripod design and spaced 7.5 cm from the centrally-located diploid or tetraploid target *S. altissima* plant (Fig. 1). The experimental designs in years 1 and 2 differed with respect to the plant source material and the number of treatments.

Year 1 - Two competition treatments: *S. altissima* plants were sampled from a natural population near Duluth MN (46.72°N, 92.03°W) and were grown in pots at UMD Research and Field Studies Area (UMD-RFSA 46.72°N, 92.04°W) for three years prior

to this experiment. *T. vulgare* clones were obtained from a naturalized population at UMD-RFSA. In May, five diploid and five tetraploid *S. altissima* genotypes were each cloned to produce 12 genets (2 ploidy levels x 5 genotypes x 12 genets = 120 target plants). Six genets were assigned to the no-competition treatment and six with the *T. vulgare*-competition treatment. The competitive *T. vulgare* plants included 30 genotypes that were each cloned to produce six genets. The six genets were split and planted into pots containing either a target diploid or tetraploid *S. altissima* plant (3 *T. vulgare* genets x 2 *S. altissima* ploidy levels x 5 *S. altissima* genotypes x 6 blocks = 180 clones). Clones that died within four days were replaced from their respective genotype. The 11.35-liter pots containing ProMix Bx (Premier® ProMix BX®) were organized in a randomized block design with six blocks (Fig. 2). Pots were watered and weeded as necessary and spread to prevent shading of target plants in the no-competition treatment.

Year 2: Three competition treatments: An intraspecific-competition treatment was added in Year 2 where diploid and tetraploid target *S. altissima* plants were grown in competition with diploid *S. altissima*. Diploids were chosen because sufficient plant material was available. All *S. altissima* plants were sampled from a natural population in Hubbard Co. MN (47.23°N, 94.88°W) that had been reared in pots at UMD-RFSC for two years prior to this experiment. In May, target *S. altissima* plants including five diploid and five tetraploid genotypes were cloned to produce 18 genets assigned to one of the following three treatments: 1) no competition, 2) interspecific competition with *T. vulgare*, or 3) intraspecific competition with diploid *S. altissima* (2 ploidy levels x 5 genotypes x 3 competition treatments x 6 blocks = 180 total target *S. altissima* plants)

(Fig. 1). *T. vulgare* plants were sampled from the Year 1 experiment and included 15 genotypes each cloned to produce 12 genets (3 *T. vulgare* genets x 2 *S. altissima* ploidy levels x 5 *S. altissima* genotypes x 6 blocks = 180 total *T. vulgare* competitor clones). Diploid *S. altissima* competitors included 10 genotypes each of which was cloned to produce 18 genets assigned to pots containing diploid or tetraploid *S. altissima* target plants (3 diploid competitor *S. altissima* genets x 2 ploidy levels of target *S. altissima* plants x 5 genotypes of *S. altissima* target plants x 6 blocks = 180 total diploid competitor *S. altissima* plants). Plants were potted, organized, and maintained as in the previous year.

Measurements

Fresh rhizome weights for both species were recorded at time of transplantation, and leaf number and plant height were measured one week later. These measurements were to account for differences in initial genet size. Stem diameter (year two only), height and leaf number were measured every other week thereafter until the date when the first plant flowered. In year one, the presence of aphids on *S. altissima* was recorded in August and September. In year two aphid presence was recorded in June, July, and August. In year one, photosynthetic rate was measured using S151 IRGA Carbon Dioxide Analyzer (Qubit Systems Inc.®) on a subset of 48 *S. altissima* plants (genets of 2 diploid and 2 tetraploid genotypes). A final set of height and leaf number measurements were taken on day of flowering. In year two, the fully-expanded leaves directly below reproductive branches were collected and pressed on the date of first flower for both species to allow measurement of specific leaf area. In early October, aboveground

vegetative and reproductive biomass was collected, dried for 72 hours at 70°C, and weighed.

Data analysis

All analyses were performed in JMP Pro 10 (SAS Institute Inc. ®). End-of-season traits were analyzed using mixed model ANCOVA, and categorical (aphid presence and flowering occurrence) traits were analyzed using Logistic Regression. Plant height, leaf number, and stem diameter measured repeatedly throughout the growing season were analyzed using mixed model split-plot approach. Complete model effects for the three groups are as follows:

<u>Target <i>S. altissima</i></u>	<u>Competitive <i>T. vulgare</i></u>	<u>Competitive <i>S. altissima</i></u>
Block*	Block*	Block*
Ploidy of target <i>S. altissima</i>	Ploidy of target <i>S. altissima</i>	Ploidy of target <i>S. altissima</i>
Competition treatment	Genotype of <i>T. vulgare</i> *	Genotype of competitor <i>S. altissima</i> *
Ploidy x Competition	Ploidy x Genotype*	Ploidy x Genotype*
Genotype(ploidy) of target <i>S. altissima</i> *	Rhizome weight of <i>T. vulgare</i>	Rhizome weight of competitor <i>S. altissima</i>
Competition x Genotype(ploidy)*		
Rhizome weight of target <i>S. altissima</i>		

Starred (*) effects were random and all others are fixed effects. Traits, except categorical traits, were transformed using Box-Cox as necessary to meet ANCOVA assumptions.

Target *S. altissima* model effect ‘Competition x Genotype(ploidy)’ was omitted for days to flowering in year one and for all categorical analyses to better fit the analysis.

Photosynthetic data was analyzed using Fit Model on JMP 8.0. A $\ln(+1)$ transformation was necessary to meet assumptions of the ANCOVA model and maintain measured zero values.

RESULTS

The experimental design allowed testing for the effects of inter- and intraspecific competition from the perspective of the both the “target plant” (diploid or tetraploid *Solidago altissima* planted at the center of the pot) and “competitor plants” (diploid *S. altissima* or *Tanacetum vulgare* planted around the target plant). Because multiple ramets per genotype were included for both species, it also was possible to estimate genetic variance for traits, and more interestingly, genetic variation in the plastic responses to the competition treatments (G x E) as experienced from both sides of the competitive interaction. First, from the perspective of the target plants, I report overall differences between diploid and tetraploid *S. altissima* followed by the effect of inter- and intraspecific competition. Next, from the perspective the competitors, I report the reciprocal effects of diploid and tetraploid *S. altissima* target plants on competitors including both diploid *S. altissima* plants and *T. vulgare*.

Differences between diploid and tetraploid *S. altissima* target plants:

Although differences between the ploidy levels were weak or not apparent in the subset of genotypes used in year one, striking differences between diploids and tetraploids were evident in year two. Regardless of the competition treatment imposed in the second year, diploid and tetraploid target *S. altissima* plants expressed inherent differences for seven of ten traits even when initial rhizome weight was taken into account (Table 1). Compared to diploids, tetraploids on average were 26% taller, had 20% thicker stems, flowered 10 days later (Fig. 3A), and accrued 39% times more

biomass by the end of the growing season (Fig. 3B). In addition, a greater percentage of tetraploid plants were infested with aphids compared to diploids in June, July, and August. These trends were reinforced in analyses of biweekly repeated measures of height, leaf number, and stem diameter (ex. Leaf Number Year 1: Ploidy $F = 10.21$; $p < 0.05$, Table 2).

The effect of competitors on target *S. altissima* plants

As expected, target *S. altissima* plants grown in competition, whether with *T. vulgare* or diploid *S. altissima*, had reduced growth compared to those grown in a noncompetitive environment. There were significant differences between the competition treatments for all traits except for days to flowering in year one and SLA in year two (Table 1). Regardless of ploidal level, year one *S. altissima* plants grown in competition were 29% shorter, had 21% fewer leaves, accrued 74% less biomass, and experienced 84% reduced flowering. Target *S. altissima* grown with *T. vulgare* also had 18% reduced photosynthetic rates ($F_{1,35}=5.75$, $P = 0.02$) than those not in competition. In contrast, competition may have had beneficial effects with respect to herbivore damage. Aphid presence was reduced on target plants when other plants co-occurred in the pot. Also, when aphids were present the intensity (total numbers on a plant) of infestation was reduced when plants co-occurred in the pot. This positive side-effect of competition was especially evident among year two *S. altissima* target plants grown in competition with *T. vulgare* that had 56-82% lower aphid presence (Fig. 3C) and 39-90% reduced average aphid count than controls.

In general, interspecific competition with *T. vulgare* had a stronger effect on *S. altissima* target plants than did the intraspecific diploid competitor. For all data with a significant competition factor, the mean trait value for the intraspecific competition treatment was intermediate between the no-competition and interspecific-competition treatment. Despite this trend, only flowering occurrence and July aphid presence in year two experienced significant differences for all three treatment means. Herbivory was less severe for target *S. altissima* plants in treatment two (interspecific competition) as there was a 9-60% reduced aphid presence compared to target plants in treatment three (intraspecific competition) (Fig. 3C). Despite a reduced aphid load, treatment two plants did experience 11% reduced flowering compared to plants in treatment three (Fig. 3D). When repeated measurements taken throughout the growing season were accounted for, target *S. altissima* grown with *T. vulgare* were significantly shorter and had fewer leaves than target plants grown with intraspecific competitor (Table 2). No traits were more strongly affected by intraspecific competition compared to interspecific competition.

In contrast to expectations, diploid and tetraploid plants rarely differed in their competitive ability in the presence of *T. vulgare* (few competition x ploidy interactions, Table 1). The response of diploids and tetraploids to competition did not differ significantly for height, leaf number, days to flowering, and biomass in both years and stem diameter, SLA and all aphid surveys in year two. One instance in which diploids and tetraploids did differ in competitive ability was in the August aphid survey of year one. Diploids benefited from the presence of *T. vulgare* more so than tetraploids (Table 1, Fig. 3C). Aphid infestation on diploids was reduced from 53% without *T. vulgare* to 0%

with *T. vulgare*. There was less of a reduction for tetraploids (33% without *T. vulgare* to 17% with *T. vulgare*). This pattern was also evident in patterns of flowering; both competitive treatments reduced flowering by 16% for diploids, but only competition with *T. vulgare* reduced likelihood of flowering for tetraploids by 20% (Table 1, Fig. 3D). Surprisingly, no other traits showed differences between the ploidy levels of target *S. altissima* in their response to competition with *T. vulgare* (Table 1).

Significant differences between the genotypes within ploidy levels were found for all traits except height, leaf number, and biomass in year one and July aphid presence in year two. In a few instances, these genotypes also responded to the competition treatments in different ways (Table 1, Competition x Genotype(Ploidy)). As an example of genetic variation in plastic response to competition, some tetraploid genotypes maintained height even in the presence of *T. vulgare* competition (e.g. Genotype 4N-4, Fig. 4A), whereas others were negatively affected by *T. vulgare* competition. There was less variation among diploid genotypes in their plastic responses to competition. Generally, diploid genotypes had poor growth in the presence of both competitors (Fig. 4 B & D).

The effect of ploidy level of target plants on diploid *S. altissima* competitors

For more than half of the traits measured, the ploidy level of the target plant in the intraspecific competitive arrays had a significant effect on growth of the diploid *S. altissima* competitors (Table 3). In all cases where the ploidy factor was significant, tetraploid target plants reduced the growth of diploid competitors more than did diploid

target plants. For example, competitive *S. altissima* grown with tetraploid target *S. altissima* accrued 26% less biomass, were 6% shorter, had 5% smaller specific leaf area, and had 6% fewer leaves compared to plants grown with diploids (Table 3, Fig. 5 A-D). Target *S. altissima* ploidy level did not significantly cause the date of first flowering to shift and it also did not have a direct impact on aphid infestation.

There were significant differences between genotypes of diploid *S. altissima* competitors for height, leaf number, SLA, day of first flower, and July aphid survey (Table 3). In only one end-of-season trait did competitor *S. altissima* genotypes significantly differ depending on target *S. altissima* ploidal pairing. Presence of aphids in July on competitive *S. altissima* genotypes significantly varied depending on target *S. altissima* ploidal pairing (Table 3). Interestingly, the competitive diploid *S. altissima* plants with aphids present varied in infestation intensity depending on target *S. altissima* ploidal level. More aphids were found on plants paired with tetraploids than plants paired with diploids. Repeated measures of height, leaf number, and stem diameter within a competitive diploid *S. altissima* genotype varied during the whole season depending on whether they were grown with a diploid or a tetraploid target *S. altissima* (Table 4).

The effect of diploid and tetraploid target plants on *T. vulgare* competitors

There were significant differences in four of six traits depending on ploidy level of the target *S. altissima* evidenced in year two but none in year one. Overall *T. vulgare* grown with diploid target *S. altissima* were more successful competitors compared to *T. vulgare* grown with tetraploids. As seen in competitive *S. altissima*, *T. vulgare* grown

with tetraploid *S. altissima* accrued 34% less biomass, were 21% shorter, had 14 thinner stems, and had 16% fewer leaves than *T. vulgare* grown with diploids (Table 5, Fig. 5 E-H). Specific leaf area and days to first flower did not differ significantly (Table 5).

Significant differences were found between *T. vulgare* genotypes in all end-of-season traits (plant height, leaf number, total biomass, flowering occurrence) in year one and two of seven traits in year two. Genotypes of *T. vulgare* differed in SLA and days to first flower in year two (Table 5). Also, the response to diploid or tetraploid *S. altissima* differed significantly depending on genotype of *T. vulgare* for all end-of-season traits in year one but for no traits in year two (Table 5). However, *T. vulgare* genotypes' response to *S. altissima* ploidal level did differ in repeated measurements of plant height, leaf number, and stem diameter for both years (Table 6). Some *T. vulgare* genotypes were more successful competitors against diploid *S. altissima*, while others were more successful when paired with tetraploid *S. altissima* in terms of plant height and leaf number (Fig. 6).

Flowering occurrence in year two and aphid presence for both years were not analyzed. Just a few *T. vulgare* replicates did not flower in year two, leaving very little power to detect statistical difference. Only one aphid was ever observed on a *T. vulgare* plant in three different surveys in year two.

DISCUSSION

These experiments show that the genetic structure of interacting species influences the competitive dynamics between native diploid and tetraploid cytotypes of *Solidago altissima* and the invasive species *Tanacetum vulgare*. Overall, there was significant genetic variation for most traits measured on experimental plants, including 70% of the traits measured on *S. altissima* and 60% of the traits measured on *T. vulgare*. Beyond this basic requirement for adaptive evolution, we also found that specific genotypes of each species responded differently to the presence of the other species (genetically-based variation in plasticity). Genetic variation in the response to contrasting environments (competition treatments in this case) indicates that adaptive phenotypic plasticity can evolve which would permit these species to contend with the presence of the other.

Because genetic variation for traits and plasticity in traits (G x E) was found on both sides of the competitive interaction, there is potential for coevolution to occur as these species interact over time. For example, the presence of an invasive species may impose selection on a native species, and the presence of genetic variation permits the native species to evolve either through fixed genetic changes or through genetically-based plastic responses. This potential for evolution of plasticity differed among diploids and tetraploids. In general, diploid *S. altissima* genotypes responded consistently negatively to competition, especially interspecific competition with *T. vulgare*. Interestingly, this was not the case with tetraploid genotypes. There were some tetraploid genotypes in both years that were not affected or were less affected by competition (e.g.

Genotype 4N-4, Fig. 2 A & C). Thus, there is more potential for tetraploids to evolve adaptive plasticity in response to the presence of *T. vulgare*. Others have found variation in competitive abilities among genotypes where certain dominant genotypes in a native population may reduce the population's susceptibility to invasion (Crutsinger et al. 2008, Leger and Espeland 2010).

This study confirms the expectation that competition, whether intra- or interspecific, affects plant growth. More importantly, this experiment demonstrated that interspecific competition with *T. vulgare* affects *S. altissima* growth more strongly than intraspecific competition with a diploid conspecific. We found a consistent trend in which target plants in the no-competition treatment had the most robust growth and reproduction compared to target plants in the intraspecific competition treatment, which were intermediate, and target plants in the interspecific competition treatment were the least vigorous.

The ultimate fitness consequences of interspecific competition for target plants are not as straightforward as it might seem. For example, all three competition treatments differed significantly for the degree of aphid infestation, but the lowest levels of infestation were in the interspecific competition treatment. Aphid infestation is used as a measure of herbivory, which is known to greatly affect fitness in *S. altissima* (Meyer 2000). Thus, it may be that *T. vulgare* has a positive influence on *S. altissima* fitness by deterring herbivores. *T. vulgare* is known to have floral compounds that are deterrents to Colorado potato beetles (Schearer 1984). It is possible that *S. altissima* plants that co-occur with *T. vulgare* will experience reduced herbivore damage because of essential oils

of *T. vulgare* that act as an insect repellent (Scheerer 1984, Chiasson et al. 2001, Palsson et al. 2008).

Despite the benefit of reduced herbivore damage that was conferred by the presence of *T. vulgare*, target plants in the interspecific competition treatment flowered in lower abundance and initiated flowering at a later date. Both of these responses could reduce the overall fitness of a population. Flowers are an important component of plant reproduction, and the amount of sexual reproduction is an important determinant of the speed of local adaptation (Barrett 2008). Furthermore, late-flowering genotypes may fail to reproduce if pollinators favor plants that flower either early or at the peak of flowering, as has been demonstrated in other systems (Elzinga 2007). Failure of late-flowering genotypes to reproduce would result in a loss of genetic variation and, subsequently, reduce the fitness of the population.

Although diploid and tetraploid target plants differed in their response to *T. vulgare* for a few traits (e.g. aphid presence and flowering occurrence), these patterns were neither consistent across years nor evident in each survey within a year. Generally, the negative affect of competition by *T. vulgare* did not differ between ploidy levels although there was a tendency for tetraploids to be less negatively affected than diploids. We expected that tetraploids would have greater competitive ability because they are 26% taller, accrued 39% times more biomass, and possess greater potential for unique gene expression patterns because of genome duplication. However, this did not translate to a significant finding of greater competitive advantage against invasive *T. vulgare*. Although surprising, this result is not unprecedented; a study on diploid and hexaploid

Aster amellus also reported a lack of difference in the competitive ability of different ploidy levels (Münzbergova 2007). However, in contrast to our results, most previous studies report higher competitive ability in polyploids (Maceira et al. 1993, Sugiyama 1998, Walck et al. 2001, Thébault et al. 2011).

Interestingly, when the data are analyzed from the perspective of the competitors, the ploidy level of the *S. altissima* target plants had consistent and strong effects. In almost all cases, competitor plants, whether intra- or interspecific, had more growth reduction if reared with a tetraploid target plant compared to a diploid target plant. The lack of evidence for significant tetraploid competitive ability on the target plant side of the interaction may be due to the fact that only one or two genotypes within tetraploids showed strong competitive ability against *T. vulgare*. Thus the total average response of all tetraploid genotypes was not found to be significantly different from the total response of all diploid genotypes.

Implications for natural populations

The genetic architecture of a native population is important for determining its competitive ability against a non-native invader. In this study, both the ploidy level and the specific genotype within the ploidy level of *S. altissima* influenced the outcome of the competitive interaction. Overall, diploid populations of *S. altissima* may be more susceptible to invasion than tetraploid populations given their reduced growth when *T. vulgare* is present. It is likely that a native population composed mainly of tetraploid *S. altissima* would be more effective at limiting the growth of competitors than a population

composed entirely of diploids. However, it is important to bear in mind that the significance of ploidy in determining competitive ability is likely to be species dependent. There was a strong effect of *S. altissima* ploidy on competitor growth, but this may not be true for other polyploid species (te Beest *et al.* 2012).

As seen in target *S. altissima*, this study provides evidence that competitor genotypes, specifically for the interspecific competitor *T. vulgare*, vary in their response to ploidal level of *S. altissima*. This suggests competitive interactions between these native and invasive species could result in selection that favors genotypes of *T. vulgare* that can maintain fitness regardless of the ploidy level of the competitor it encounters. Not all competitors are created equally; just as in the native species, some genotypes of the invasive species are better competitors than others. Thus, the genotype of both the native species and the invader can be a significant factor in invasion dynamics. This study provides strong evidence that competitive interactions should be viewed from multiple perspectives to inform our understanding of the complex interplay between specific genotypes of interacting species.

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TABLES

Table 1. Target *Solidago altissima* plants: ANCOVA and nominal logistic test statistics on measurements taken on diploid and tetraploid target *S. altissima* genotypes grown in the center of a pot with: 1) no competition, 2) interspecific competition with *T. vulgare*, and 3) intraspecific competition with diploid *S. altissima* (treatment 3 in year two only). † $p \leq 0.10$; * $p \leq 0.05$; ** $p \leq 0.001$; *** $p \leq 0.0001$

	Ploidy of Target <i>S. altissima</i>		Competition		Ploidy x Competition		Genotype(Ploidy) ¹		Competition x Genotype(Ploidy) ¹		Initial rhizome weight ²		Block ¹	
	<i>F/X</i> ²	<i>df</i>	<i>F/X</i> ²	<i>df</i>	<i>F/X</i> ²	<i>df</i>	<i>F/X</i> ²	<i>df</i>	<i>F</i>	<i>df</i>	<i>F/X</i> ²	<i>df</i>	<i>F/X</i> ²	<i>df</i>
Year One														
<i>Height</i>	0.35	1, 9 ⁵	20.41*	1, 8 ⁵	0.19	1, 8 ⁵	1.31	8, 8 ⁵	3.16*	8, 94	29.12***	1, 94	2.59*	5, 94
<i>Leaf #</i> ³	3.37†	1, 9 ⁵	51.52***	1, 8 ⁵	0.12	1, 8 ⁵	1.71	8, 8 ⁵	1.92†	8, 94	12.61**	1, 94	0.80	5, 94
<i>Days to Flower</i>	0.02	1, 18 ⁵	0.003	1, 26	0.00	1, 26	4.39*	8, 26	—	—	5.03*	1, 26	0.56	5, 26
<i>Biomass</i> ⁴	0.55	1, 9 ⁵	82.32***	1, 8 ⁵	0.01	1, 8 ⁵	0.87	8, 8 ⁵	2.00†	8, 94	29.74***	1, 94	2.00†	5, 94
<i>Flower (y/n)</i>	0.21	1	52.78***	1	0.25	1	29.45**	8	—	—	2.92†	1	7.54	5
<i>Aug Aphid (y/n)</i>	0.00	1	28.71***	1	13.15**	1	19.61*	8	—	—	3.65†	1	9.54†	5
<i>Sept Aphid (y/n)</i>	0.00	1	62.92***	1	0.72	1	21.59*	8	—	—	2.65	1	11.72*	5
Year Two														
<i>Height</i>	10.50*	1, 8 ⁵	22.50***	2, 16 ⁵	0.21	2, 16 ⁵	3.84*	8, 17 ⁵	1.87*	16, 144	44.69***	1, 144	3.00*	5, 144
<i>Leaf #</i> ⁴	0.54	1, 8 ⁵	45.37***	2, 16 ⁵	1.48	2, 16 ⁵	8.72***	8, 17 ⁵	1.25	16, 144	20.21***	1, 144	1.23	5, 144
<i>Stem diameter</i>	5.82*	1, 8 ⁵	46.34***	2, 16 ⁵	0.44	2, 16 ⁵	7.58**	8, 17 ⁵	1.48	16, 144	64.57***	1, 144	1.18	5, 144
<i>SLA</i> ³	3.23	1, 8 ⁵	0.03	2, 16 ⁵	1.89	2, 16 ⁵	9.92***	8, 18 ⁵	0.87	16, 144	0.74	1, 144	0.32	5, 144
<i>Days to Flower</i> ⁴	9.44*	1, 8 ⁵	5.05*	2, 17 ⁵	0.18	2, 17 ⁵	11.53***	8, 17 ⁵	1.58†	16, 125	13.97**	1, 125	0.62	5, 125
<i>Biomass</i> ⁴	5.97*	1, 8 ⁵	73.44***	2, 16 ⁵	0.14	2, 16 ⁵	5.59**	8, 17 ⁵	1.13	16, 144	40.54***	1, 144	0.46	5, 144
<i>Flower(y/n)</i>	0.00	1	20.12⁶***	2	7.93*	2	35.43***	8	—	—	21.06***	1	3.08	5
<i>June Aphid (y/n)</i>	32.90***	1	27.63***	2	3.33	2	34.56***	8	—	—	10.04*	1	40.55***	5
<i>July Aphid (y/n)</i>	42.59***	1	27.13⁶***	2	3.71	2	6.15	8	—	—	9.01*	1	4.97	5
<i>Aug Aphid (y/n)</i>	5.96*	1	11.17*	2	2.26	2	15.54*	8	—	—	0.99	1	8.96	5

¹ Random effect; ² Box-Cox $\lambda = 0$ transformed in year one, $\lambda = 0.5$ transformed in year two; ³ Box-Cox $\lambda = 0$ transformed; ⁴ Box-Cox $\lambda = 0.5$ transformed;

⁵ Degrees of freedom approximated, ⁶ All three competition treatments significantly different from each other

Table 2. Target *Solidago altissima* plants: Repeated measures of height, leaf number, and stem diameter (year two only) on diploid and tetraploid target *S. altissima* genotypes grown with: 1) no competition, 2) interspecific competition with *T. vulgare*, and 3) intraspecific competition with diploid *S. altissima* (treatment 3 in year two only). † $p \leq 0.10$; * $p \leq 0.05$; ** $p \leq 0.001$; *** $p \leq 0.0001$

	Ploidy		Competition		Ploidy x Competition		Genotype(Ploidy) ¹		Competition x Genotype(Ploidy) ¹		Initial rhizome weight ²		Block ¹			
	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>		
Year One																
Height ³	0.05	1, 8 ⁵	10.95*	1, 8 ⁵	0.07	1, 8 ⁵	1.91	8, 9 ⁵	22.93***	8, 32	209.21***	1, 470	19.51***	5, 20		
Leaf # ⁴	10.21*	1, 8 ⁵	121.71***	1, 8 ⁵	0.44	1, 8 ⁵	2.84*	8, 19 ⁵	5.32**	8, 32	185.76***	1, 470	15.34***	5, 20		
Year Two																
Height	0.44	1, 8 ⁵	25.32***	2, 16 ⁵	1.42	2, 16 ⁵	5.23**	8, 27 ⁵	6.69***	16, 32	272.12***	1, 432	10.57**	5, 10		
Leaf # ⁴	1.44	1, 8 ⁵	25.50***	2, 16 ⁵	0.97	2, 16 ⁵	8.31***	8, 29 ⁵	9.91***	16, 32	218.09***	1, 432	2.11	5, 10		
Stem diameter	6.88*	1, 8 ⁵	52.85***	2, 16 ⁵	0.65	2, 16 ⁵	10.37***	8, 18 ⁵	18.48***	16, 16	197.93***	1, 288	12.43*	5, 5		
	Time . . .		x Ploidy		x Competition		x Ploidy x Competition		x Genotype(Ploidy) ¹		x Competition x Genotype(Ploidy) ¹		x Initial rhizome weight ³⁽²⁾		x Block ¹	
	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>
Year One																
Height ³	962.04***	4, 3 ⁵	0.23	4, 43 ⁵	40.09***	4, 31 ⁵	0.20	4, 32 ⁵	2.33*	32, 40 ⁵	0.38	32, 470	0.19	4, 470	0.41	20, 470
Leaf # ⁴	211.58***	4, 9 ⁵	0.20	4, 39 ⁵	91.92***	4, 31 ⁵	0.44	4, 32 ⁵	4.14***	32, 41 ⁵	0.36	32, 470	0.91	4, 470	0.32	20, 470
Year Two																
Height	287.10***	2, 11 ⁵	1.93	2, 16 ⁵	55.44⁶***	4, 33 ⁵	0.79	4, 31 ⁵	8.07***	16, 44 ⁵	0.27	32, 432	3.73*	2, 432	0.79	10, 432
Leaf # ⁴	66.39***	2, 15 ⁵	2.68†	2, 16 ⁵	39.23⁶***	4, 32 ⁵	11.81***	4, 32 ⁵	9.62***	16, 40 ⁵	0.39	32, 432	2.34†	2, 432	1.12	10, 432
Stem diam	0.56	1, 5 ⁵	1.10	1, 11 ⁵	22.84***	2, 17 ⁵	1.62	2, 15 ⁵	1.56	8, 33 ⁵	0.10	16, 288	0.23	1, 288	0.77	5, 288

¹ Random effect; ² Box-Cox $\lambda = 0.5$ transformed in year two, $\lambda = 0$ transformed in year one; ³ Box-Cox $\lambda = 0$ transformed; ⁴ Box-Cox $\lambda = 0.5$ transformed; ⁵ Degrees of freedom approximated; ⁶ All 3 treatments significantly different from each other

Table 3. Intraspecific Competitor *Solidago altissima* plants: ANCOVA and nominal logistic test statistics on measurements on the intraspecific *S. altissima* competitor (all diploid) that were planted around a diploid or tetraploid target *S. altissima* plant in year two. † $p \leq 0.10$; * $p \leq 0.05$; ** $p \leq 0.001$; *** $p \leq 0.0001$

Factor	Target <i>S. altissima</i> Ploidy		Competitor Genotype ¹		Target <i>S. altissima</i> Ploidy x Competitor Genotype ¹		Initial rhizome weight ²		Block ¹	
	<i>F/X</i> ²	<i>df</i>	<i>F/X</i> ²	<i>df</i>	<i>F/X</i> ²	<i>df</i>	<i>F/X</i> ²	<i>df</i>	<i>F/X</i> ²	<i>df</i>
Height ³	6.96*	1, 8 ⁵	3.46*	9, 10 ⁵	0.76	9, 35	6.62*	1, 35	0.52	4, 35
Leaf # ²	13.83*	1, 8 ⁵	5.29*	9, 10 ⁵	0.57	9, 35	5.75*	1, 35	0.95	4, 35
Stem diameter ⁴	20.45*	1, 6 ⁵	2.76†	9, 12 ⁵	0.15	9, 35	6.51*	1, 35	0.50	4, 35
SLA	9.05*	1, 8 ⁵	7.52*	9, 10 ⁵	0.82	9, 35	1.67	1, 35	0.44	4, 35
Day of 1 st Flower	1.94	1, 8 ⁵	7.38*	9, 10 ⁵	0.70	9, 35	4.48*	1, 35	1.21	4, 35
Biomass ²	8.47*	1, 8 ⁵	2.44†	9, 10 ⁵	0.70	9, 35	4.39*	1, 35	0.37	4, 35
June Aphid (y/n)	0.00	1	12.65	9	5.20	9	0.51	1	11.66*	4
July Aphid (y/n)	0.00	1	34.05***	9	20.49*	9	5.63*	1	21.78**	4
Aug Aphid (y/n)	0.00	1	12.94	9	3.81	9	0.02	1	7.34	4

¹ Random effect

² Box-Cox $\lambda = 0$ transformed

³ Box-Cox $\lambda = 0.5$ transformed

⁴ Box-Cox $\lambda = -2$ transformed

⁵ Degrees of freedom approximated

Table 4. Intraspecific competitor *Solidago altissima* plants: Repeated measurements of height, leaf number, and stem diameter of intraspecific diploid competitor *S. altissima* grown around diploid and tetraploid Target *S. altissima* in year two. † $p \leq 0.10$; * $p \leq 0.05$; ** $p \leq 0.001$; *** $p \leq 0.0001$

	Target <i>S. altissima</i> ploidy		Competitor Genotype ¹		Target <i>S. altissima</i> ploidy x Competitor Genotype ¹		Initial rhizome weight ²		Block ¹	
	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>
Height ²	0.54	1, 9 ⁴	4.02*	9, 11 ⁴	11.49***	9, 18	29.04***	1, 105	25.67***	4, 8
Leaf # ²	5.63*	1, 9 ⁴	6.25**	9, 24 ⁴	6.37**	9, 18	11.90**	1, 105	13.05**	4, 8
Stem Diameter ³	6.80*	1, 8 ⁴	3.08†	9, 9 ⁴	4.74*	9, 9	21.72***	1, 70	5.99†	4, 4

Time . . .	x Target <i>S. altissima</i> ploidy		x Competitor Genotype ¹		x Target <i>S. altissima</i> ploidy x Competitor Genotype ¹		x Initial rhizome weight ²		x Block ¹			
	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>		
Height ²	545.61***	2, 15 ⁴	3.66†	2, 14 ⁴	2.23*	18, 22 ⁴	0.24	18, 105	0.17	2, 105	0.13	8, 105
Leaf # ²	34.60***	2, 9 ⁴	0.86	2, 13 ⁴	11.10***	18, 22 ⁴	0.22	18, 105	0.19	2, 105	0.26	8, 105
Stem Diameter ³	99.31***	1, 6 ⁴	1.89	1, 6 ⁴	1.21	9, 12 ⁴	0.19	9, 70	0.09	1, 70	0.22	4, 70

¹ Random effect

² Box-Cox $\lambda = 0$ transformed

³ Box-Cox $\lambda = 0.5$ transformed

⁴ Degrees of freedom approximated

Table 5. Interspecific Competitor *Tanacetum vulgare* plants: ANCOVA and nominal logistic test statistics on measurements taken on the interspecific competitor *T. vulgare* planted around diploid and tetraploid target *S. altissima* for two years. Thirty genotypes were used in year one and 15 in year two. There were no shared replicates among blocks in year one, thus block effect is only applicable in year two. † $p \leq 0.10$; * $p \leq 0.05$; ** $p \leq 0.001$; *** $p \leq 0.0001$

Factor	Target <i>S. altissima</i> Ploidy		Competitor Genotype ¹		Target <i>S. altissima</i> Ploidy x Competitor Genotype ¹		Initial rhizome weight ²		Block ¹	
	<i>F/X</i> ²	<i>df</i>	<i>F/X</i> ²	<i>df</i>	<i>F/X</i> ²	<i>df</i>	<i>F/X</i> ²	<i>df</i>	<i>F/X</i> ²	<i>df</i>
Year One										
<i>Height</i>	0.74	1, 29 ⁶	2.95*	29, 29 ⁶	3.17***	29, 119	114.81***	1, 119	—	—
<i>Leaf #</i> ³	0.00	1, 29 ⁶	2.33*	29, 29 ⁶	2.89***	29, 119	25.92***	1, 119	—	—
<i>Biomass</i> ³	0.09	1, 29 ⁶	3.88**	29, 29 ⁶	1.59*	29, 119	83.50***	1, 119	—	—
<i>Flower (y/n)</i>	0.00	1	136.26***	29	37.63***	29	42.24***	1	—	—
Year Two										
<i>Height</i>	7.70*	1, 14 ⁶	1.11	14, 14 ⁶	1.50	14, 26	0.29	1, 26	0.21	3, 26
<i>Leaf #</i> ²	9.62*	1, 13 ⁶	1.53	14, 15 ⁶	0.90	14, 26	0.72	1, 26	0.69	3, 26
<i>Stem diameter</i> ²	10.24*	1, 13 ⁶	0.95	14, 15 ⁶	1.04	14, 26	0.16	1, 26	0.87	3, 26
<i>SLA</i> ⁵	1.47	1, 13 ⁶	10.12***	14, 15 ⁶	0.76	14, 26	0.90	1, 26	2.94†	3, 26
<i>Days to 1st Flower</i> ³	0.36	1, 12 ⁶	13.42***	13, 15 ⁶	0.35	13, 23	4.25†	1, 23	1.45	3, 23
<i>Biomass</i> ²	5.26*	1, 13 ⁶	1.01	14, 15 ⁶	1.07	14, 26	0.16	1, 26	1.40	3, 26

¹ Random effect

² Box-Cox $\lambda = 0$ transformed

³ Box-Cox $\lambda = 0.5$ transformed

⁵ Box-Cox $\lambda = -1$ transformed

⁶ Degrees of freedom approximated

Table 6. Interspecific competitor *Tanacetum vulgare* plants: Repeated measurements of height, leaf number, and stem diameter (year two only) on interspecific competitor *T. vulgare* genotypes grown around both diploid and tetraploid Target *S. altissima* for both years. There were no shared replicates among blocks in year one, thus block effect is only applicable in year two. † $p \leq 0.10$; * $p \leq 0.05$; ** $p \leq 0.001$; *** $p \leq 0.0001$

	Target <i>S. altissima</i> ploidy		Competitor Genotype ¹		Target <i>S. altissima</i> ploidy x Competitor Genotype ¹		Initial rhizome weight ²		Block ¹			
	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>		
Year One												
Height ³	0.13	1, 29 ⁵	5.34***	29, 49 ⁵	11.10***	29, 116	533.88***	1, 595	—	—		
Leaf # ²	0.13	1, 29 ⁵	3.28***	29, 58 ⁵	4.23***	29, 116	344.58***	1, 595	—	—		
Year Two												
Height ²	5.75*	1, 14 ⁵	2.77*	14, 15 ⁵	21.51***	14, 42	7.80*	1, 104	0.29	3, 9		
Leaf # ⁴	9.77*	1, 14 ⁵	3.62*	14, 16 ⁵	4.69***	14, 42	1.59	1, 104	3.10†	3, 9		
Stem Diameter ²	8.68*	1, 14 ⁵	1.62	14, 14 ⁵	8.47***	14, 28	4.60*	1, 78	1.14	3, 6		
Time . . .	x Target <i>S. altissima</i> ploidy		x Competitor Genotype ¹		x Target <i>S. altissima</i> ploidy x Competitor Genotype ¹		x Initial rhizome weight ²		x Block ¹			
	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>df</i>		
Year One												
Height ³	576.77***	4, 113 ⁵	0.92	4, 114 ⁵	4.53***	116, 125 ⁵	0.32	116, 595	12.92***	4, 595	—	—
Leaf # ²	226.82***	4, 114 ⁵	0.43	4, 115 ⁵	3.13***	116, 120 ⁵	0.75	116, 595	11.00***	4, 595	—	—
Year Two												
Height ²	920.99***	3, 30 ⁵	5.25*	3, 33 ⁵	1.64*	42, 53 ⁵	0.18	42, 104	0.02	3, 104	0.12	9, 104
Leaf # ⁴	11.56*	3, 9 ⁵	2.15	3, 40 ⁵	1.34	42, 44 ⁵	0.91	42, 104	0.84	3, 104	1.82†	9, 104
Stem Diameter ³	62.67***	2, 25 ⁵	1.41	2, 24 ⁵	0.95	28, 33 ⁵	0.30	28, 78	0.11	2, 78	0.24	6, 78

¹ Random effect; ² Box-Cox $\lambda = 0$ transformed; ³ Box-Cox $\lambda = 0.5$ transformed; ⁴ Box-Cox $\lambda = -1$ transformed; ⁵ Degrees of freedom approximated

FIGURES

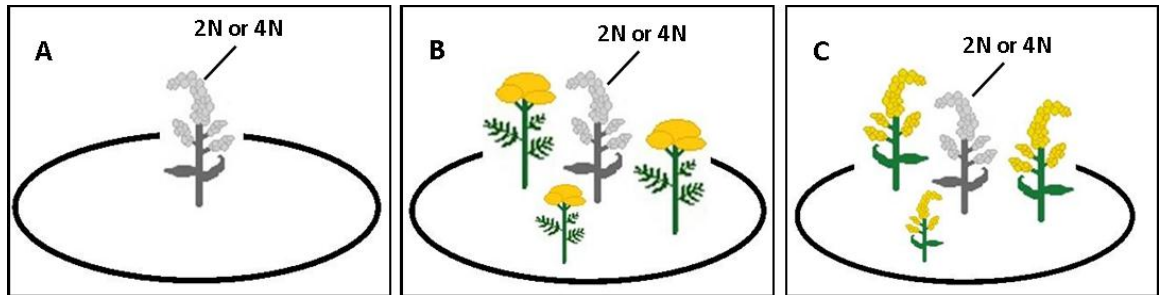


Figure 1. Representation of one pot in each of three competition treatments: (A) No-competition, a single diploid or tetraploid *S. altissima* target plant grown singly; (B) Interspecific competition, one diploid or tetraploid *S. altissima* target plant grown with three *T. vulgare* clones of the same genotype; and (C) Intraspecific competition, a single diploid or tetraploid *S. altissima* target plant grown with three diploid *S. altissima* clones of the same genotype.

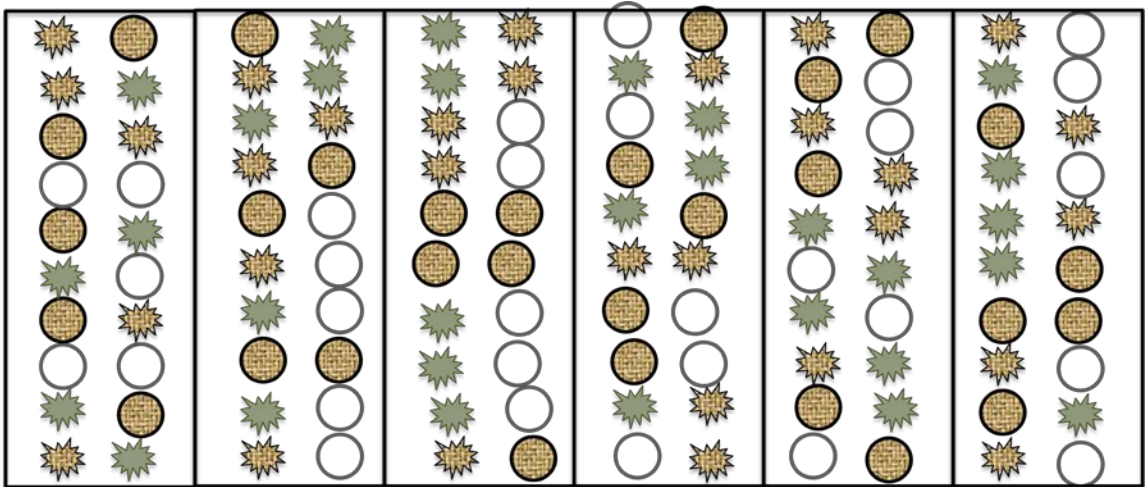


Figure 2. Representation of 6 randomized blocks in year one. Circles indicate pots in no-competition treatment; spiked bubbles indicated pots intraspecific competition treatment. Open dots indicated diploid target plants while textured dots indicate tetraploid pots. Pots were staggered to minimize shading from other pots

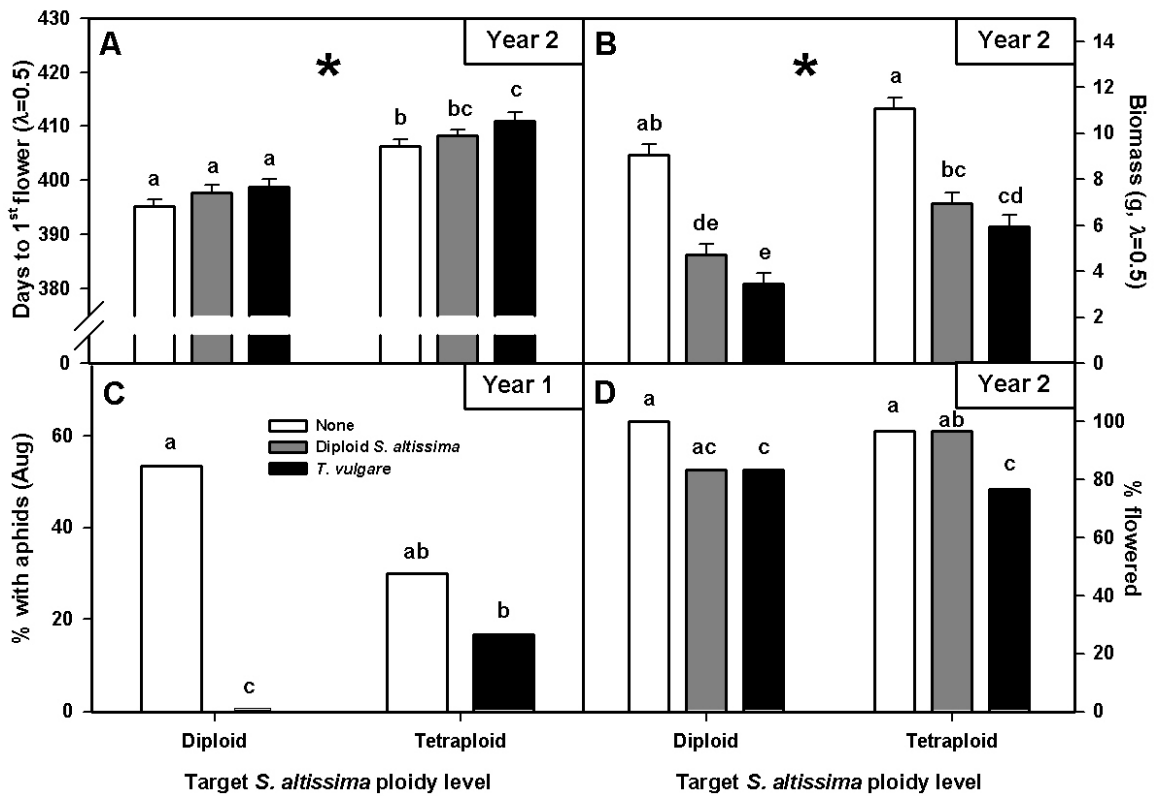


Figure 3. Data showing the effect of three competitive treatments on target *S. altissima* including: No competition (white bars), competition with diploid *S. altissima* (grey bars), and competition with *T. vulgare* (black bars) on (A) flowering time, (B) total biomass production (C) August aphid infestation, and (D) % of plants that flowered (LSM \pm SE). Stars indicate where the ploidy level also differed significantly (* $p < 0.05$). There was no evidence of ploidy effect on aphid infestation (C) and % flowering occurrence (D), but each competition treatment mean was significantly different according to chi-squared tests.

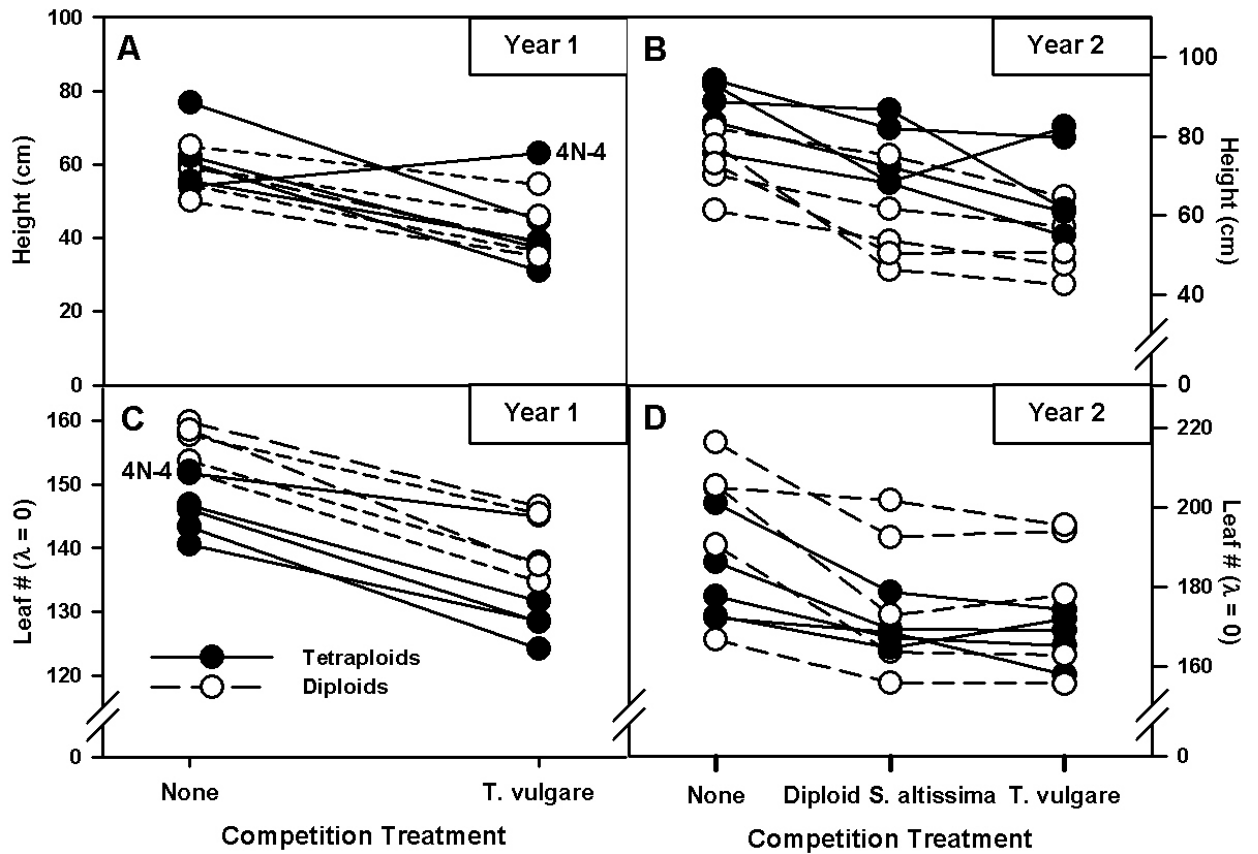


Figure 4. Effect of inter- and intraspecific competition on diploid (open circles) and tetraploid (closed circles) target *S. altissima* plants. Lines represent one genotype. Significant differences in the plastic response of genotypes within ploidy level were evident for traits associated with plant size in both years: height (A) year one and (B) year two; (D) leaf number year one and (D) year two (see Supplemental Table 3 for year two data).

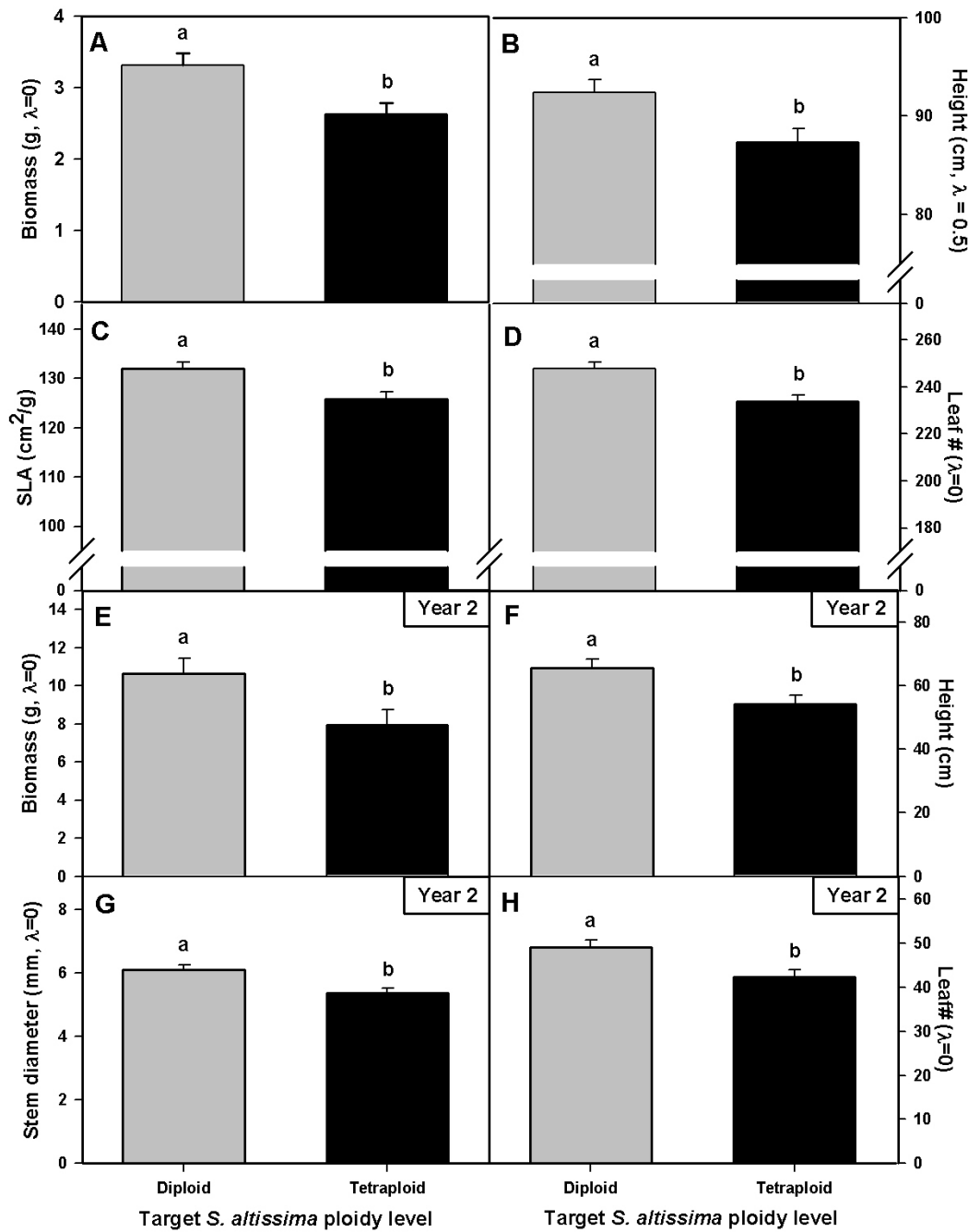


Figure 5. The effect on competitor fitness by ploidal level of target *S. altissima*. Intraspecific competitor *S. altissima* differed significantly in (A) total biomass, (B) final height, (C) SLA, and (D) final leaf number depending on pairing with diploid or tetraploid target *S. altissima*. Interspecific competitor *T. vulgare* significantly differed on (E) total biomass, (F) final height, (G) final stem diameter, and (H) final leaf number depending on target *S. altissima* ploidal level.

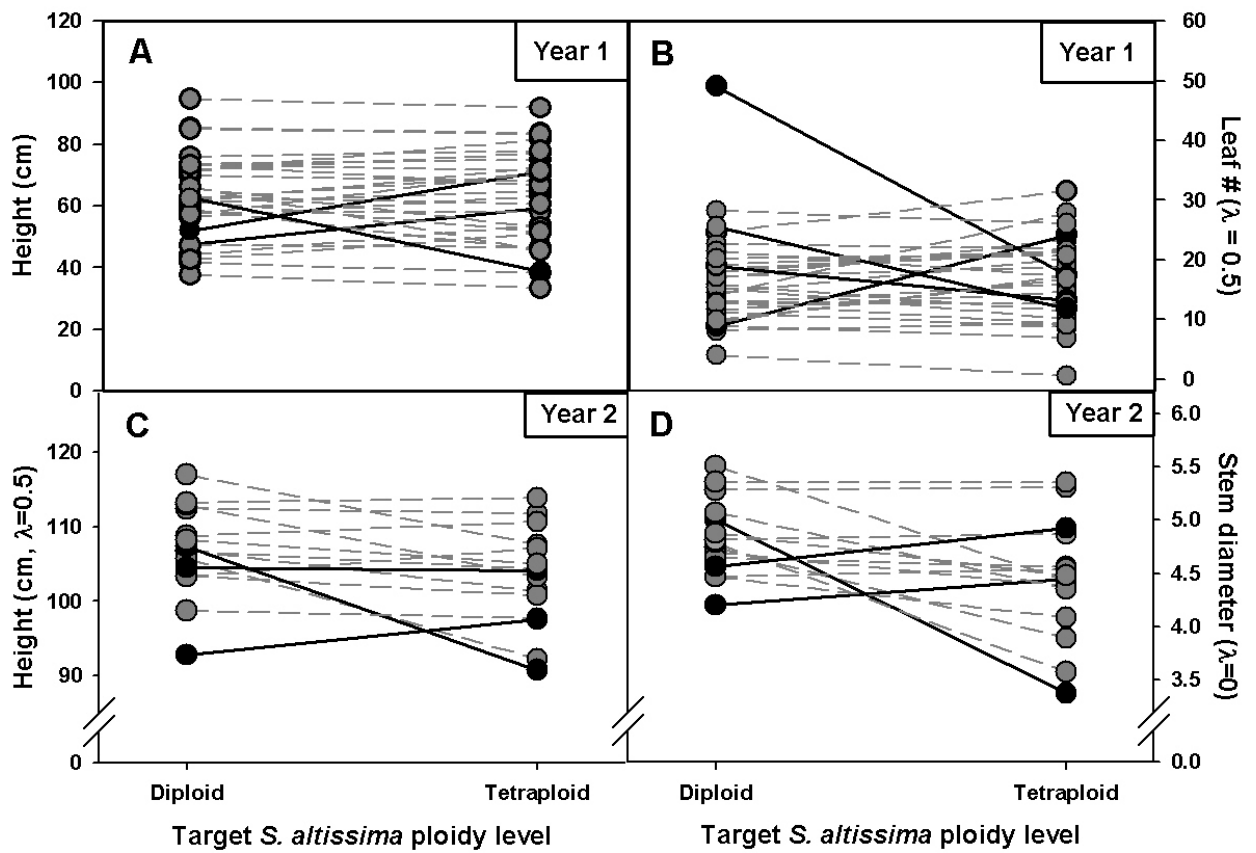


Figure 6. Effect on genotypes of *T. vulgare* depending on pairing with diploid or tetraploid target *S. altissima*. Significant differences in year one were (a) height and (b) leaf number, and in year two collective (c) height and (d) stem diameter at the end of the growing season.